PROBLEMATICAL FOSSIL CNIDARIANS FROM THE UPPER ORDOVICIAN OF THE NORTH-CENTRAL USA

by HEYO VAN ITEN, JULIE ANN FITZKE *and* ROBT S. COX

ABSTRACT. *Sphenothallus* sp. and eight species of conulariids, distributed among the genera *Climacoconus*, *Conularia*, *Glyptoconularia* and *Metaconularia*, occur in the Elgin Member of the Maquoketa Formation (upper Ordovician) of north-eastern Iowa and south-eastern Minnesota, USA. Seven of the eight conulariid species exhibit internal test structures at their corners and/or midlines. Comparisons of these test structures with internal thecal structures of coronatid scyphozoans corroborate the hypothesis that conulariids were more closely related to scyphozoan cnidarians than they were to any other extant taxon of comparable rank. *Sphenothallus* and conulariids occur in all four Elgin Member biofacies. However, the distribution of *Climacoconus* and *Conularia* is facies-dependent, with *Climacoconus* occurring predominantly in the brachiopod-echinoderm biofacies and the basal Maquoketa phosphorite, *Conularia splendida* predominantly in the trilobite-dominated biofacies, and *C. trentonensis* predominantly in the brachiopod-echinoderm, mixed faunas and graptolite shales biofacies. Conulariids commonly occur in monospecific clusters, possibly clonal in origin, and some specimens show orientational evidence of original attachment to *Sphenothallus* or nautiloid shell material. Together with previously reported data on the distribution and biostratinomy of *Sphenothallus* and conulariids, these results suggest that both taxa were sessile benthic organisms that inhabited all major Elgin Member bottom environments, including a shallow, oxic carbonate shelf and a deeper, dysoxic shelf margin and shale basin slope. One new species, *Climacoconus sinclairi*, is described.

CONULARIIDS and their possible close relative *Sphenothallus* Hall, 1847 are widely distributed in Palaeozoic marine strata and are often mutually associated. Both may occur in exceptional abundance in certain rock units. Among the best known units previously discussed are the middle Ordovician Šárka and Dobrotivá formations of Bohemia (conulariids; e.g. Havlíček 1966), the upper Ordovician May Sandstone of Brittany (conulariids; e.g. Bouček 1928) and the upper Ordovician Collingwood Formation of Ontario and Quebec (conulariids and *Sphenothallus*; e.g. Bolton 1994). *Sphenothallus* and conulariids often occur in dark shales and lime mudstones in which normal marine taxa such as echinoderms and articulate brachiopods are rare or absent. Together with evidence suggesting that *Sphenothallus* and conulariids were sessile benthic organisms (e.g. Bodenbender *et al.* 1989; Van Iten 1991*b*), such occurrences raise the possibility that these taxa were capable of living in bottom waters subject to oxygen depletion and/or other forms of stress.

Recent analyses of large numbers of *Sphenothallus* and conulariid specimens from deposits such as those mentioned above have substantially increased our knowledge of anatomical variation within these organisms, and have provided evidence bearing on alternative interpretations of their mode of life and life history (e.g. Bodenbender *et al.* 1989; Van Iten 1991*c*, 1992*a*; Van Iten *et al.* 1992; Jerre 1993, 1994). This work has also contributed to discussions of the phylogenetic affinities of these taxa, one or both of which have been variously interpreted as annelids or other 'worms' (*Sphenothallus* and conulariids; e.g. Clarke 1913; Moore *et al.* 1952; Mason and Yochelson 1985; Fauchald *et al.* 1986; Babcock 1991), hemichordates or chordates (conulariids; Termier and Termier 1949, 1953; Steul 1984), an independent phylum (conulariids; e.g. Kozlowski 1968; Babcock and Feldmann 1986*a*; Babcock 1990, 1991; Yochelson 1991) or close relatives of hydrozoan or scyphozoan cnidarians (*Sphenothallus* and conulariids; e.g. Price 1920; Kiderlen

[Palaeontology, Vol. 39, Part 4, 1996, pp. 1037–1064, 3 pls]

1937; Moore and Harrington 1956; Chapman 1966; Werner 1966, 1967; Glaessner 1971, 1984; Bischoff 1978; Grasshoff 1984; Van Iten 1991*a*, 1992*a*, 1992*b*, 1992*c*; Van Iten and Cox 1992; Van Iten *et al.* 1992; Jerre 1994).

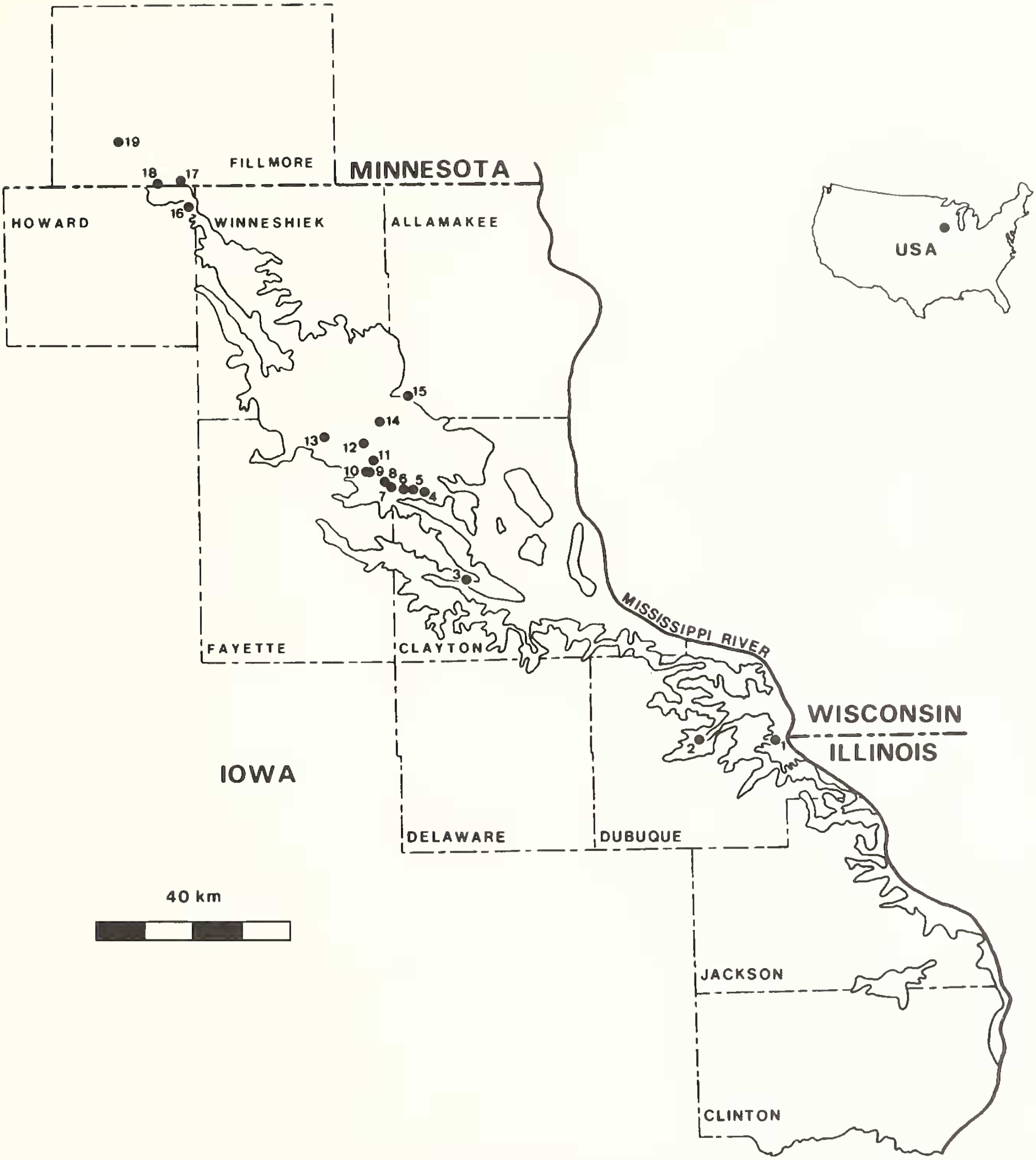
The present paper addresses the taxonomy and palaeoecology of *Sphenothallus* and conulariids in the Elgin Member of the Maquoketa Formation (upper Ordovician) of north-eastern Iowa and south-eastern Minnesota, USA. The purpose of this study is to document the exceptionally diverse Elgin *Sphenothallus*/conulariid fauna and to interpret aspects of the anatomy and distribution of these taxa having an important bearing on discussions of their affinities and palaeoecology. The Maysvillian (late Caradoc) Elgin Member has long been known for its abundant trilobites, echinoderms, brachiopods and molluscs (e.g. Slocum 1914; Slocum and Foerste 1920; Walter 1924; Ladd 1929; Miller and Youngquist 1949; Tasch 1955; Bretsky and Bermingham 1970; Whittington 1971). Until now, however, this unit had not been recognized as a major *Sphenothallus*/conulariid horizon. The Elgin Member contains eight species of conulariids representing the genera *Climacoconus* Sinclair, *Conularia* Miller *in* Sowerby, *Glyptoconularia* Sinclair and *Metaconularia* Foerste. One species is new. With the possible exceptions of the middle Ordovician Trenton Group of New York and Quebec and the lower Silurian Manitoulin Dolomite of northern Michigan and south-western Ontario (Sinclair 1948), no other North American stratigraphical unit contains as many conulariid genera and species as does the Elgin Member.

The Elgin Member consists of intertonguing shales and carbonates deposited in a density-stratified epeiric sea the bottom waters of which were dysoxic or anoxic over large areas (Witzke 1980, 1987; Witzke and Kolata 1989). Coupled with the unusually high diversity and abundance of Elgin *Sphenothallus* and conulariids, the substantial facies variation of this unit makes it an attractive setting for the analysis of the palaeoecology of these two groups. In particular, conulariids have been variously interpreted as sessile benthic (e.g. Babcock *et al.* 1987*a*, 1987*b*; Van Iten 1991*a*, 1991*b*), nektonic (e.g. Havlíček 1966) or planktonic or pseudoplanktonic organisms (e.g. Ruedemann 1934; Babcock and Feldmann 1984, 1986*b*). As will be discussed below, conulariids occur in all Elgin facies, but the distribution of conulariid species is facies-dependent. Moreover, conulariid specimens may occur in undisturbed life clusters or preserve orientational evidence of primary apical attachment to nautiloid shells and *Sphenothallus* tubules.

MATERIALS AND METHODS

The present study is based on direct examination of specimens collected from over 20 localities in the northern and central parts of the Maquoketa outcrop belt of north-eastern Iowa and south-eastern Minnesota (Text-fig. 1; Appendix 1). The sample consists of approximately 350 macroscopic specimens, mostly conulariids, and minute (about 1 to 2 mm long) conulariid and *Sphenothallus* test fragments (e.g. Pl. 2, fig. 2) obtained by dissolving pieces of limestone approximately 1 kg in mass in 4N formic acid. Test fragments were picked from undissolved residues washed on a 63 μm brass screen. The limestone samples (Appendix 2) were collected in place, at 1 m intervals, from localities (4, 8, 16–17 and 19) that together expose most of the currently recognized stratigraphical units within the carbonate portion of the member. Test fragment samples are housed in the Department of Geology, State University of Iowa, under collection number 84492.

Abbreviations of North American institutions housing specimens examined in this study are as follows: AC, Augustana College, Rock Island, Illinois; AMNH, American Museum of Natural History, New York; CCPC, Department of Geology, Carleton College, Northfield, Minnesota; FMNH, Field Museum of Natural History, Chicago; GSC, Geological Survey of Canada, Ottawa; NYSM, New York State Museum, Albany; SUI, State University of Iowa, Iowa City; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; UMPC, University of Minnesota Paleontology Collections, Minneapolis; WSU, Winona State University, Winona, Minnesota.



TEXT-FIG. 1. Map of the Maquoketa Formation/Elgin Member (upper Ordovician) outcrop belt in north-eastern Iowa and south-eastern Minnesota, USA. Numbered dots represent collecting localities that yielded *Sphenothallus* and/or conulariid specimens examined in the present study (see Appendix 1).

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

Maquoketa Formation

The Maquoketa Formation (considered to be a group by stratigraphers in Illinois, Indiana and Wisconsin; e.g. Gray 1972; Sivon 1980; Kolata and Graese 1983) ranges from Maysvillian to Richmondian (Caradoc to Ashgill) and underlies much of the north-central United States east of the Transcontinental Arch (Witzke 1980, 1987; Witzke and Kolata 1989). The formation consists of two major facies: cherty shelf carbonates, preserved mainly in the subsurface and extending from eastern Iowa to the Transcontinental Arch; and shale-dominated strata developed east and south of this region, primarily in south-eastern Wisconsin, Illinois, Indiana, north-eastern Missouri and eastern Iowa. Shale-dominated strata occur at the surface primarily in south-eastern Wisconsin, western Illinois, north-eastern Missouri, south-eastern Minnesota and north-eastern Iowa. In north-eastern Iowa and south-eastern Minnesota, these beds range from about 30 to 100 m thick and crop out sporadically in a narrow, north-west–south-east-trending belt that extends from north-eastern Clinton County, Iowa to southern Fillmore County, Minnesota (Parker *et al.* 1959; Parker 1971; Text-fig. 1). In most of the north-western half of the outcrop belt the Maquoketa Formation consists of five members. Listed in ascending order, these are the Elgin Shaly Limestone, the Clermont Shale, the Fort Atkinson Limestone, the Brainard Shale and the Neda Shale. Due in part to pre-mid Devonian erosion, only the Elgin Member is present in Minnesota. South of a line extending through southernmost Clayton and Fayette counties, Iowa, the Elgin Member consists mainly of dark shales, and the rest of the Maquoketa Formation is composed almost entirely of lighter-coloured shales assigned to the Brainard Member. In both north-eastern Iowa and south-eastern Minnesota, the Maquoketa (Elgin Member) rests conformably on shaly limestones of the upper Ordovician Dubuque Formation, while the top of the formation is marked by an unconformity overlain by lower Silurian dolostones (north-eastern Iowa) or middle Devonian limestones (south-eastern Minnesota).

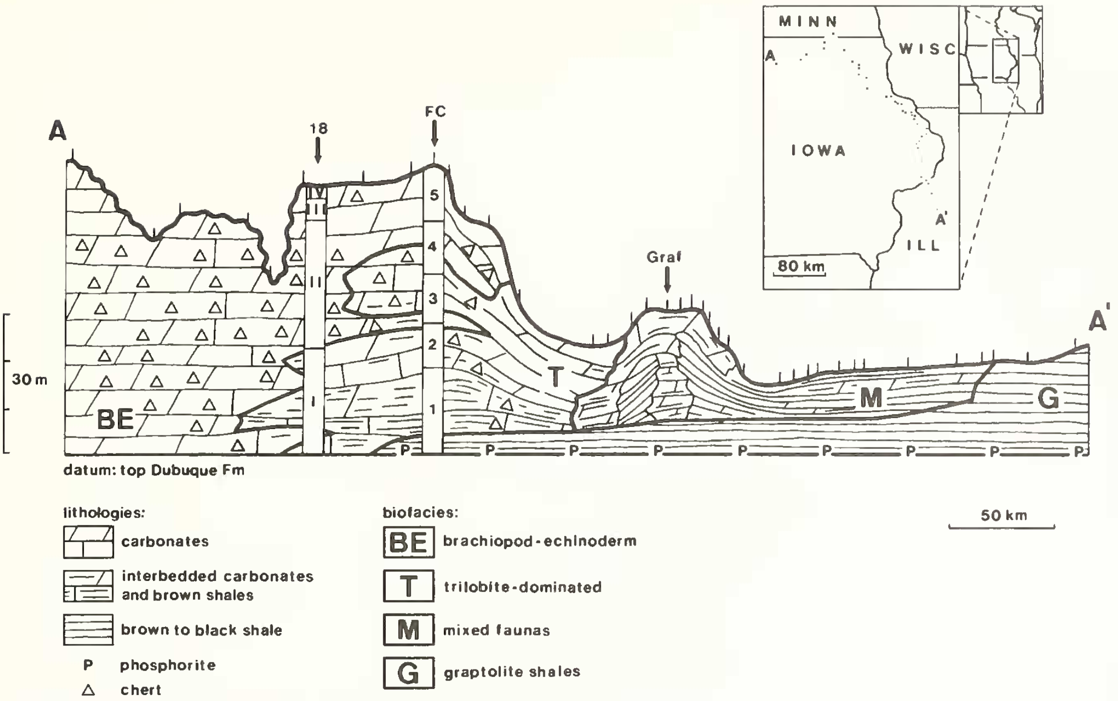
Elgin Member

The Elgin Member in the Iowa/Minnesota outcrop belt represents a shallowing-upward sequence showing maximum facies variation along a north-west–south-east transect (Witzke 1980, 1987; Text-fig. 2). Except in Minnesota, where Maquoketa strata have been deeply eroded, the Elgin Member is conformably overlain by shales of the Clermont or Brainard members. In the Iowa/Minnesota border area, in southernmost Fillmore County, Minnesota and the northernmost parts of Howard and Winneshiek Counties, Iowa, the Elgin consists predominantly of grey and light grey biomicrites and has been subdivided into four subunits, designated Lithosomes I–IV (Bayer 1967; Elias *et al.* 1988; Text-fig. 2). Lithosome I is characterized by a sparse, low diversity macrofauna dominated by graptolites and the trilobite *Isotelus iowensis* Owen. Lithosomes II and III are cherty and contain abundant, diverse invertebrate faunas including articulate brachiopods, pelecypods, nautiloids, trilobites, crinoids, sponges and solitary rugose corals.

South of the Iowa/Minnesota border area, in a region encompassing parts of south-eastern Winneshiek, south-western Allamakee, north-eastern Fayette and north-western Clayton counties, Iowa, the Elgin Member consists predominantly of thin biomicrites interbedded with brown graptolitic shales. Elgin Member strata can be subdivided over much of this area into five units, designated Units 1–5 (Parker *et al.* 1959; Text-fig. 2). Unit 1 is separated from the underlying Dubuque Formation by a thin phosphate horizon, the basal Maquoketa phosphorite, that occurs at the base of the Elgin Member throughout most of north-eastern Iowa. Units 1–3 are similar palaeontologically to Lithosome I, while Units 4 and 5 contain diverse macrofaunas consisting of abundant trilobites as well as articulate brachiopods, nautiloids, gastropods, crinoids, cystoids and sponges.

In the southern part of the Maquoketa outcrop belt, in south-eastern Fayette, southern Clayton and eastern Dubuque, Jackson and Clinton counties, Iowa, the Elgin Member consists mostly of brown to grey or black, graptolitic shales with locally abundant inarticulate brachiopods (*Lingula*) and rare trilobites (Text-fig. 2). In the vicinity of the village of Graf, north-eastern Dubuque County, the upper part of the unit exhibits numerous thin interbeds of dolostone containing abundant nautiloids and rare crinoids and bryozoans.

The lithological units described above together define four mutually intertonguing biofacies (Witzke 1980, 1987; Text-fig. 2). Moving from north-west to south-east, these are (1) the brachiopod-echinoderm biofacies (Lithosomes II and III of Bayer 1967; Units 4 and 5 of Parker *et*



TEXT-FIG. 2. North-west–south-east stratigraphical cross section of the Elgin Member of the Maquoketa Formation (upper Ordovician) in north-eastern Iowa and south-eastern Minnesota, USA. Stratigraphical column labelled 'FC' represents the Fitzgerald Creek measured section of Parker *et al.* (1959, fig. 2b); stratigraphical column labelled '18' (Locality 18) represents the measured section of Bayer (1967, fig. 2). Text-figure modified from Witzke (1987, fig. 4).

al. 1959); (2) the trilobite-dominated biofacies (Lithosome I of Bayer 1967; Units 1–3 of Parker *et al.* 1959); (3) the mixed faunas biofacies (alternating brown to black graptolitic shales and phosphatic dolomites); and (4) the graptolite shales biofacies (brown to black graptolitic shales stratigraphically below and lateral to the mixed faunas beds). These four biofacies were originally deposited in 'contrasting water masses of a stratified epicontinental seaway' (Witzke 1987, p. 239), in 'three general bathymetric settings: (1) shallow carbonate shelf [brachiopod-echinoderm biofacies]; (2) shelf margin (deepening to the southeast) [trilobite-dominated and mixed faunas biofacies]; and (3) basin slope [graptolite shales biofacies]' (Witzke 1987, p. 237). The shallow carbonate shelf, represented by Lithosomes II and III and Units 4 and 5, was deposited in areas where a well-mixed, oxic upper water mass impinged on the sea floor. Deposition here was generally below fair-weather wave base but above storm wave base (Elias *et al.* 1988). On more proximal parts of the shallow carbonate shelf, sandy lime muds lacking benthic organisms (Lithosome IV) were deposited in waters that were highly restricted. Below the oxic upper water mass, in the proximal shelf slope environment, asaphid-graptolite mudstones of the trilobite-dominated biofacies were deposited in the upper part of a zone of increasing density and decreasing oxygen content, or pycnocline. Deposition of the grey to dark grey, pyritic asaphid-graptolite mudstones of Unit 1 and Lithosome I probably occurred in dysoxic waters. The distal shelf slope, largely deposited in lower pycnoclinal waters that were further depleted in oxygen, was the site of graptolitic shale sedimentation (lowermost mixed faunas facies and brown to grey organic shales of the graptolite shales biofacies). Below the pycnocline, deposition of grey to black laminated shales commonly lacking benthic invertebrates (parts of the graptolite shales biofacies) took place at the base of a relatively deep water mass that was dysoxic to anoxic.

Based on these interpretations of depositional environments and on inspection of exposures showing transitions between facies, we propose the following chronostratigraphical correlations of Elgin Member subunits. As suggested by Witzke (1980), the basal Maquoketa phosphorite in north-eastern Iowa probably represents a condensed interval that correlates with Lithosome I and laterally equivalent parts of Lithosome II in south-eastern Minnesota. Units 1–3 of the trilobite-dominated biofacies can be correlated with Lithosome III and the upper part of Lithosome II (see for example Bayer's (1967) measured section for Locality 18 (Bayer Locality F-231)) and with the lower part of the graptolite shales biofacies (including units 1–3 of Witzke and Glenister's (1987, fig. 3) Graf, Iowa section). Finally, Units 4 and 5 probably correlate with Lithosomes III and IV and with the mixed faunas and upper graptolite shales biofacies (in southern Clayton County, Unit 4 may pass southward into strata assignable to Unit 3).

ANATOMICAL TERMINOLOGY

Use of anatomical terminology in this paper is generally consistent with precedents to be found in Sinclair (1940, 1942, 1952), Moore and Harrington (1956) and Van Iten (1992*a*). Two new terms, both pertaining to test features of *Conularia*, are introduced here. As indicated by inspection of sectioned and broken material, the interspaces (the regions between the crests of the transverse ribs) of most currently recognized species of *Conularia* are longitudinally corrugated (Pl. 3, figs 1, 3). The crests of the corrugations (as seen viewing the test's exterior surface) will be referred to as interspace ridges, while the troughs between the crests will be referred to as interspace furrows.

SYSTEMATIC PALAEONTOLOGY

Phylum CNIDARIA Hatschek, 1888
Class, Order, Family Uncertain

Genus SPHENOTHALLUS Hall, 1847

Sphenothallus sp.

Plate 1, figure 8; Plate 2, figure 1

Material. SUI 84486, 84493b, 84495i–k, 84496, 84497a, 84498, 84499a, 84500, 84514e–f, 84517b (> 50 specimens).

EXPLANATION OF PLATE 1

Figs 1, 6. *Conularia splendida* Billings, 1866; upper Ordovician, Maquoketa Formation, Elgin Member, Unit 1; near the mouth of Otter Creek in Elgin, Fayette County, Iowa, USA. 1, SUI 49979a; external view of two faces of a flattened but more or less complete specimen; ×1·7. 6, SUI 49979; radial cluster of eight specimens, all of which are oriented parallel to bedding and occur in a grey, pyritic lime mudstone with graptolites and asaphid trilobite fragments; ×0·66.

Fig. 2. *Conularia trentonensis* Hall, 1847; SUI 61508; upper Ordovician, Maquoketa Formation, Elgin Member, ?Unit 3; north-eastern Iowa (Locality 16), USA; external view of two faces of a flattened specimen; ×1·6.

Fig. 3. *Conularia*? sp.; SUI 84491; upper Ordovician, Maquoketa Formation, Elgin Member, Lithosome II; south-eastern Minnesota (Locality 18), USA; internal mould of a partial face and two corners; ×2.

Figs 4, 8. *Climacoconus quadratus* (Walcott, 1879); upper Ordovician, Maquoketa Formation, Elgin Member, Lithosome I; south-eastern Minnesota, USA. 4, SUI 84494; Locality 18; external view of two faces and a corner; ×2·6. 8, SUI 84493a; Locality 19; partial external moulds of two specimens oriented with their apex next to a tubule of *Sphenothallus* sp. (SUI 84493b); ×4·3.

Fig. 5. *Glyptoconularia gracilis* (Hall, 1847); SUI 55065; upper Ordovician, Maquoketa Formation, Elgin Member, mixed faunas biofacies; north-eastern Iowa (Locality 2), USA; external mould of part of a face and two corners; ×4·7.

Fig. 7. *Climacoconus sinclairi* sp. nov.; GSC 94784; upper Ordovician, Maquoketa Formation, Elgin Member, Unit 3; north-eastern Iowa (Locality 11), USA; external view of the holotype; ×3·1.

PLATE 1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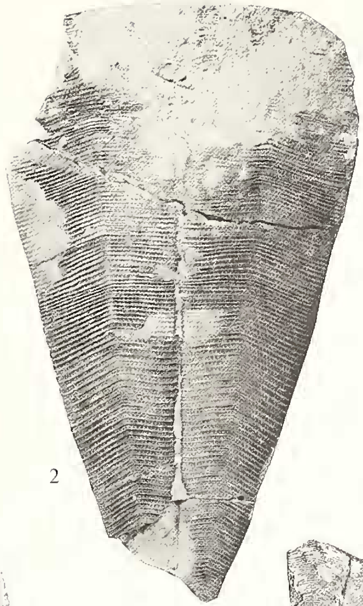
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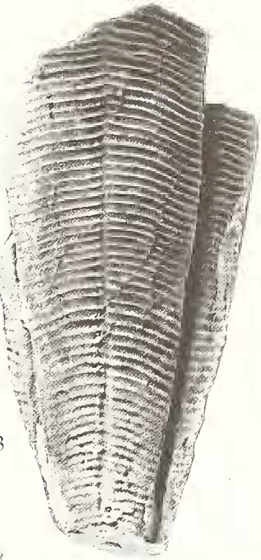
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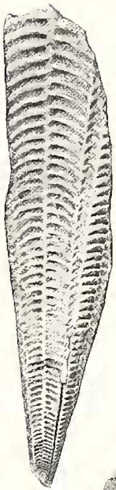
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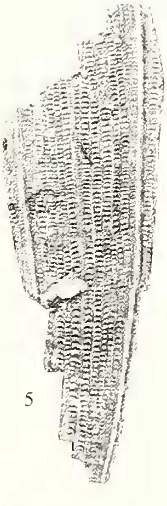
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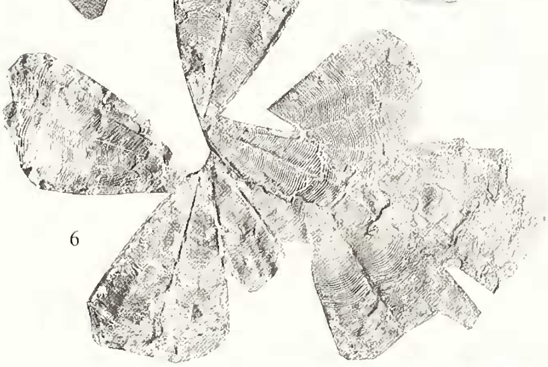
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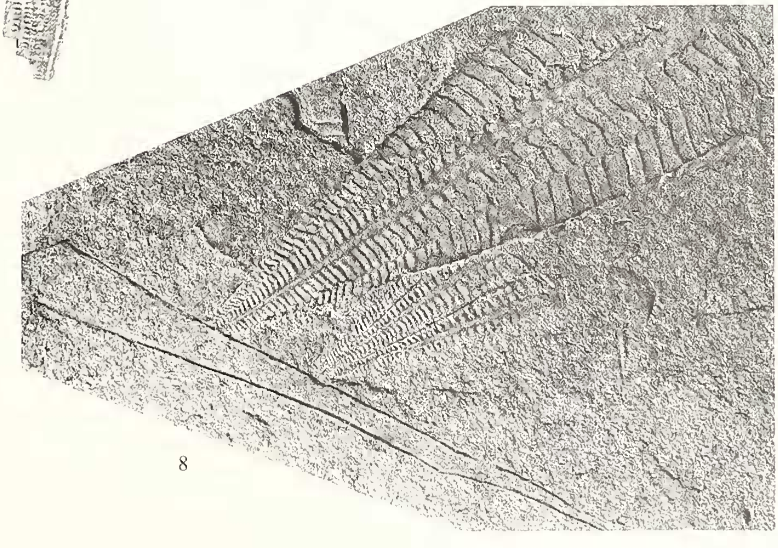
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VAN ITEN *et al.*, *Conularia*, *Climacoconus*, *Glyptoconularia*

Horizon and localities. Elgin Member, Lithosome II (Localities 17b and 19), mixed faunas biofacies (Locality 2; bed 8 of Witzke and Glenister (1987, fig. 3)), graptolite shales biofacies (Locality 1).

Description. Partial tubules up to 90 mm long; tubules apatitic, finely lamellar, preserving one or both longitudinal thickenings and, in some cases, small portions of the thin wall between the thickenings; tubules gently tapered and strongly curved near the apical end; holdfasts not preserved.

Remarks. *Sphenothallus* is widely distributed in middle and upper Ordovician strata of North America, where it is represented by at least two species, *S. angustifolius* Hall (the type species) and *S. splendens* (Hall) (Bolton 1994). The Elgin Member specimens, while similar to these two species in size and gross anatomy, are not sufficiently complete to allow detailed comparisons of the thin test wall between the longitudinal thickenings. As indicated by previous discussions of *Sphenothallus* morphology (e.g. Mason and Yochelson 1985; Van Iten *et al.* 1992; Bolton 1994), this relatively delicate part of the tubule shows interspecific variation in the development of surface ornament. For these reasons, the Elgin Member specimens are here left unassigned at the species level.

It is interesting to note that none of the Elgin Member *Sphenothallus* specimens examined in this study preserves the holdfast. Abundant *Sphenothallus* with holdfasts have been found in mudrocks at several other localities, including the Lower Carboniferous Calciferous Sandstone of Scotland (Slater 1907) and Bear Gulch Limestone of central Montana (Van Iten *et al.* 1992). Some of the specimens from the Calciferous Sandstone are attached to conulariids (*Paraconularia tenuis* (Slater)), while those from the Bear Gulch Limestone commonly are attached to ammonoid shells. In addition to these specimens, abundant non-mineralized holdfasts, similar in gross anatomy and microstructure to mineralized *Sphenothallus* holdfasts, and interpreted by Bodenbender *et al.* (1989) as *Sphenothallus* remains, have been found attached to hardground surfaces in the upper Ordovician Dillsboro Formation of Ohio.

Genus CLIMACOCONUS Sinclair, 1942

Climacoconus sinclairi sp. nov.

Plate 1, figure 7; Plate 2, figure 4; Text-figure 3A

1992*a* *Climacoconus* sp. Van Iten, p. 341, text-fig. 3g.

Derivation of name. In honour of the late George Winston Sinclair, a leading student of conulariids and author of the genus *Climacoconus*.

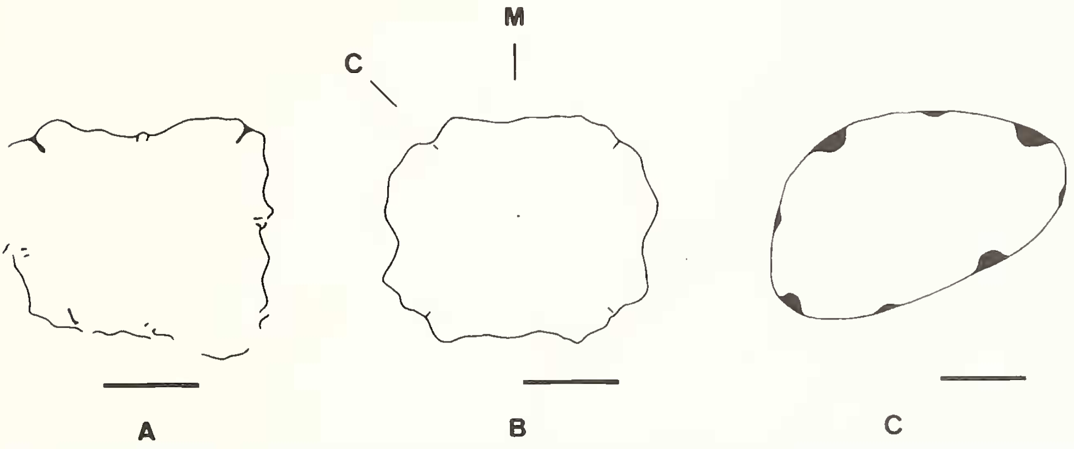
Types. Holotype, GSC 94784; paratypes, SUI 61531, 84487; Elgin Member, Units 3 (Localities 5, 11 and 14) and 5 (Locality 10).

Diagnosis. Midlines straddled internally by a pair of closely spaced, adaperturally diverging files of low, discrete, I-shaped ridges that each extend across an interspace.

Description. Three partial specimens, all broken well above the apex. Corners of a given face diverge at about 14°; corner grooves thickened, carinate; corner carina low, keel-like, darker in colour than the rest of the test; exterior surface of the corner grooves crossed by extremely fine, closely spaced, adaperturally arching transverse wrinkles that number about 25 per mm. Transverse ribs usually alternate at the midlines, straight within about 15 mm of the apex, elsewhere gently curved; transverse ribs increase in size and spacing adaperturally, numbering 6 per 2 mm about 15 mm above the apex and 4 per 2 mm about 25 mm above the apex; transverse ribs offset and deflected toward the aperture on the margins of the corner grooves; within the corner grooves the transverse ribs occur as low, broadly rounded, adaperturally arching ridges that extend approximately two-thirds of the way across the grooves and alternate with ridges projecting from the other side. Midline ridge zigzagged where the transverse ribs alternate, straight where the transverse ribs meet in opposition; midlines straddled along most of their length by a pair of closely spaced, adaperturally diverging files of low, discrete, I-shaped internal ridges, with each ridge extending across an interspace.

Comparisons. *Climacoconus sinclairi* differs from all previously published species of the genus (Sinclair 1942, 1946; Hergarten 1985) in having a pair of seriated internal carinae at the midlines. *C. sinclairi* further differs from *C. bottnicus* (Holm), *C. scoticus* (Lamont) and *C. urbanis* Sinclair in exhibiting alternation of transverse ribs at the midlines, and from *C. batteryensis* (Twenhofel) and *C. bureaui* Sinclair in having carinate corners. The new species further differs from *C. quadratus* (Walcott) in having the transverse ribs straighter.

Remarks. The holotype of *C. sinclairi* was described in an unpublished Ph.D. dissertation by Sinclair (1948), who named it *C. clermontanus* (after the village of Clermont, Fayette County, Iowa). The paired files of I-shaped midline ridges are difficult to see in this specimen (the bases of about 15 of the ridges have been exposed through exfoliation), and Sinclair (1948) did not mention them.



TEXT-FIG. 3. Camera lucida drawings of transverse cross sections through Elgin conulariids having internal test structures at their corners (C) and midlines (M). A, *Climacoconus sinclairi* sp. nov.; SUI 61531. B, *Climacoconus quadratus* (Walcott); SUI 84501. C, *Conularia*? sp.; SUI 84490. Scale bars represent 2·5 mm.

The three currently available specimens of *C. sinclairi* were collected from Unit 3. Two additional specimens, now missing, were collected by the senior author from dolostones near the base of Unit 5.

Climacoconus with paired seriated carinae at the midlines also occur in the middle Ordovician Platteville and Decorah formations near Minneapolis, Minnesota (Van Iten 1992*a*). Reposited specimens are housed in collections of the Geological Survey of Canada (GSC 94785–94786; approximately ten specimens) and the University of Michigan Museum of Paleontology (UMMP 2065; two specimens). Sinclair (1948) assigned the GSC specimens to *C. concinnus* (GSC 94785) or *C. mollis* (GSC 94686), two species erected by Sinclair (1948) but never published. These specimens and UMMP 2065 may represent *C. sinclairi*, but it will be necessary to examine more complete material before making a definitive identification.

Climacoconus quadratus (Walcott, 1879)

Plate 1, figures 4, 8; Plate 2, figure 2; Text-figure 3B

1879 *Conularia quadrata* Walcott, p. 93.
1942 *Climacoconus quadratus* (Walcott); Sinclair, p. 226, pl. 3, figs 1–5.

Material. SUI 62669, 81517–81518, 84492, 84493a, 84494, 84495a–h, 84501–84513, 84514a–d, 84515a–c (84 specimens); WSU unnumbered (six specimens).

Horizon and localities. Elgin Member, Lithosomes I and II (Localities 17b, 18 and 19), Units 1, 4 and 5 (Localities 7 and 9).

Description. Original length of the largest specimen exceeded 80 mm. Faces equal in width or with one set of opposing faces up to about 1·5 times as wide as the other two. Corners of a given face diverge at about 12–15°; corner grooves thickened, carinate; corner carina low, keel-like. Midlines also carinate; midline carina extremely low. Transverse ribs generally alternate at the midlines; transverse ribs in the apical region straight, rounded, meeting at the midlines at about 140°; elsewhere the transverse ribs have sharp crests, are gently curved and intersect the midlines at about 90°; transverse ribs increase in size and spacing adaperturally, with 12 per mm near the apex and 1 or 2 per mm approximately 80 mm above the apex; transverse ribs slightly offset on the margins of the corner grooves, deflected toward the aperture within the grooves and occurring there as low, broadly rounded, adaperturally arching ridges that extend about two-thirds of the way across the grooves and alternate with ridges extending from the other side. Midline ridge zigzagged in the apical region, becoming straighter adaperturally. Exterior of the test crossed by low, closely spaced transverse wrinkles, barely perceptible in the apical region and increasing in size and spacing adaperturally; wrinkles gently arched on the faces, strongly arched in the corner grooves.

Remarks. Climacoconus quadratus (Walcott), originally described from the Trenton Group (middle Ordovician) of New York (Walcott 1879), was interpreted by Van Iten (1992*a*) as having non-carinate midlines. Comparison of broken type specimens of this species with specimens from the Elgin Member indicates that this conclusion probably was incorrect.

Climacoconus pumilus (Ladd, 1929)

Plate 2, figures 5–6; Text-figure 3c

1929 *Conularia pumila* Ladd, p. 384.
1942 *Climacoconus pumilus* (Ladd); Sinclair, p. 231, pl. 2, fig. 10.

Material. UWBM 73175–73176 (45 specimens).

Horizon and locality. Elgin Member, basal Maquoketa phosphorite (Locality 15).

EXPLANATION OF PLATE 2

Fig. 1. *Sphenothallus* sp.; SUI 84486; upper Ordovician, Maquoketa Formation, Elgin Member, graptolite shales biofacies; north-eastern Iowa (Locality 1), USA; tubule preserving portions of both longitudinal thickenings; ×12·2.

Fig. 2. *Climacoconous quadratus* (Walcott, 1879); SUI 84492; upper Ordovician, Maquoketa Formation, Elgin Member, Lithosome II; south-eastern Minnesota (Locality 17b), USA; inner surface of a minute test fragment exhibiting part of a low internal carina at a midline; ×40.

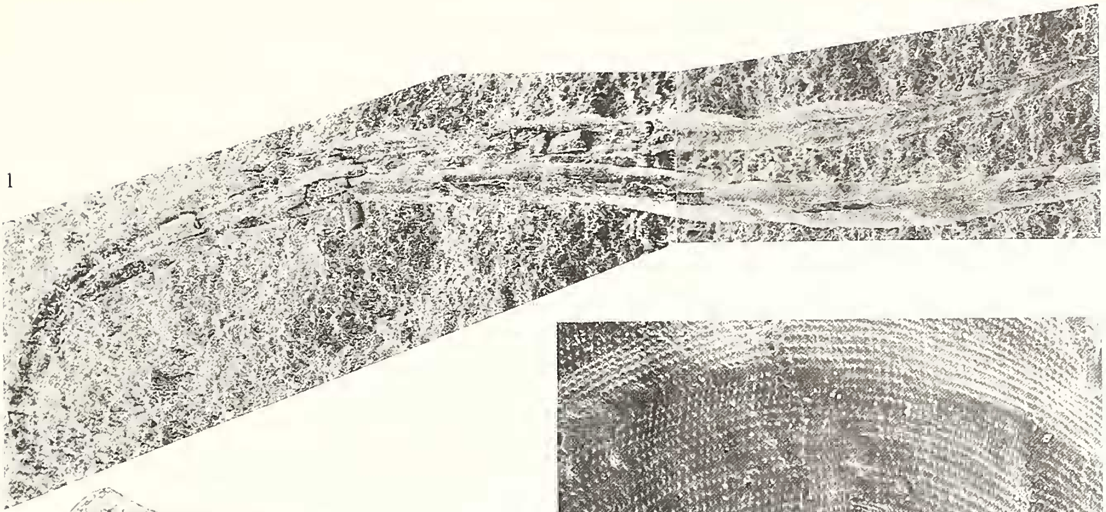
Fig. 3. *Metaconularia heymani* (Foerste, 1920); SUI 62672; upper Ordovician, Maquoketa Formation, Elgin Member, Unit 3; north-eastern Iowa (Locality 7), USA; plastic cast of part of a single face; the centre of the area shown here lies approximately 10 mm above the broken apical end (or roughly 20 mm above the former apex); ×30.

Fig. 4. *Climacoconus sinclairi* sp. nov.; SUI 84487; upper Ordovician, Maquoketa Formation, Elgin Member, Unit 3; north-eastern Iowa (Locality 5), USA; part of a double row of I-shaped internal ridges flanking a midline; ×13·2.

Figs 5–6. *Climacoconus pumilus* (Ladd, 1929); upper Ordovician, Maquoketa Formation, Elgin Member, basal Maquoketa phosphorite; north-eastern Iowa (Locality 15), USA. 5, UWBM 73175a; relatively large specimen; ×30. 6, UWBM 73175b; broken apical end of specimen showing the internal carina (arrows) at the corners; ×80.

All are scanning electron micrographs.

PLATE 2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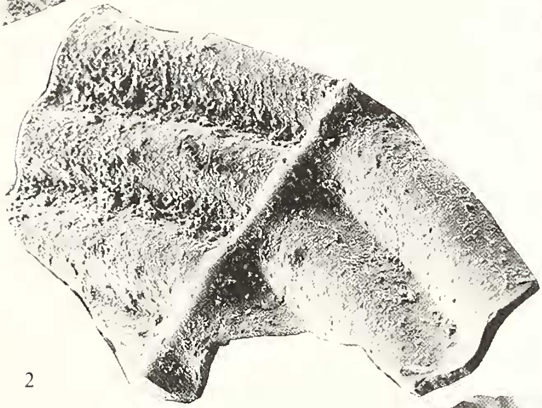
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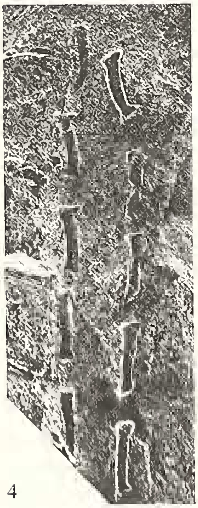
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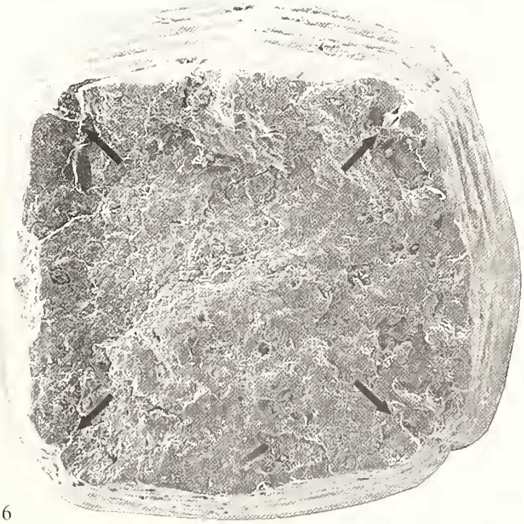
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VAN ITEN *et al.*, *Sphenothallus*, *Climacoconus*, *Metaconularia*

Description. Specimens about 1·0 to 2·5 mm long, broken at both ends but with the apical end commonly less than 0·1 mm wide. Faces equal in width or with one pair of opposing faces slightly wider than the other two. Corners of a given face diverge at about 9–10°; corner grooves narrow, angular, carinate; corner carina low, keel-like. Transverse ribs straight, rounded, alternating at the midlines and numbering 8–9 per mm. Midlines lack internal thickening, zigzag midline ridge.

Remarks. *Climacoconus pumilus* (Ladd) is similar to the apical region of *C. quadratus* (the three available specimens of *C. sinclairi* sp. nov. do not preserve this region), and as noted above the apertural end of available *C. pumilus* specimens is broken. This raises the possibility that *C. pumilus* represents the apical region of *C. quadratus* or some other species (e.g. *C. sinclairi*) having an internal carina at the corners. At this point, however, we have no grounds for rejecting the hypothesis that *C. pumilus* is a distinct species.

Genus CONULARIA Miller *in* Sowerby, 1821

Conularia trentonensis Hall, 1847

Plate 1, figure 2; Plate 3, figures 1–2

1847 *Conularia trentonensis* Hall, p. 222, pl. 59, fig. 4a–f.
1991*c* *Conularia trentonensis* Hall; Van Iten, text-fig. 2.
1992*a* *Conularia trentonensis* Hall; Van Iten, pl. 1, figs 1, 4.

Material. SUI 61506–61509, 64492, 81515, 84497b, 84499b, 84515d, 84516, 84517a, 84518–84521, 84522a (54 specimens); WSU unnumbered (seven specimens).

Horizon and localities. Elgin Member, Lithosomes I and II (Localities 17a and 18), mixed faunas biofacies (Locality 2; bed 8 or 10 of Witzke and Glenister (1987, fig. 3)), graptolite shales biofacies (Locality 2; bed 3 of Witzke and Glenister (1987, fig. 3)).

Description. Faces equal in width. Corners of a given face diverge at about 15–25°; corners and midlines lack internal thickening. Transverse ribs chevron-like on the faces, confluent at the midlines, where they form a more-or-less distinct angle that ranges from *c*. 145° to 162°; transverse ribs reduced in height and deflected toward the aperture in the corner grooves, where they consist of a single row of longitudinally elongate nodes; transverse ribs number up to 9 per mm within about 10 mm of the apex, elsewhere from 2 to 5 per mm. Rib nodes on the faces tend to be laterally elongate and widely spaced, numbering 4–9 per mm and separated by a gap that generally ranges from *c*. 1–1·5 node diameters in length. Interspace ridges commonly narrow, bar-like, about half as wide as the interspace furrows; interspace ridges extend from the base of a node on the transverse rib nearest the aperture to an area between two adjacent nodes on the transverse rib nearest the apex; interspace furrows slightly raised along their axis; interspaces crossed by coarse, closely spaced longitudinal striae in the corner grooves. Apical end of some specimens covered by a schott.

Remarks. *Conularia trentonensis* has been reported widely from the middle Ordovician of North America (Sinclair 1948). Our inspection of museum collections in Canada and the USA indicates that this species is widespread in both the middle and the upper Ordovician, and may also occur in the lower Silurian.

Conularia splendida Billings, 1866

Plate 1, figures 1, 6; Plate 3, figures 3–4

1866 *Conularia splendida* Billings, p. 21.
1927 *Conularia splendida* Billings; Twenhofel, p. 256, pl. 27, fig. 9.
1991*a* *Conularia splendida* Billings; Van Iten, p. 148, fig. 3.
1991*c* *Conularia splendida* Billings; Van Iten, text-figs 3, 4a.
1992*a* *Conularia splendida* Billings; Van Iten, pl. 2, fig. 6.

Material. AC I-1448 (one specimen); CCPC 2122.00, 2128.00 (four specimens); FMNH P16976, P16989, P17011, and P17044 (five specimens); SUI 49978, 49979, 61511–61530, 64478–64480, 64483, 64488–64491, 81516, 84522b, 84523–84535 (113 specimens); UMPC 8919 (one specimen); UWBM 73177 (one specimen).

Horizon and localities. Elgin Member, Lithosome I (Locality 18), Units 1, 2 (Localities 4, 7 and 9) and 3 (Localities 4–8, 12 and 13), graptolite shales biofacies (Localities 1–3; specimens from Locality 2 found in bed 3 of Witzke and Glenister (1987, fig. 3)).

Description. Faces equal in width or with one pair of opposing faces up to about 1·3 times as wide as the other two. Corners of a given face diverge at about 20–30°; corners lack internal thickening. Midlines with internal thickening consisting of a single carina, an adaxially bifid single carina or a pair of carinae; midline thickening commonly marked on the exterior of the test by a narrow band of light or dark colouration. Transverse ribs chevron-like within about 10 mm of the apex, elsewhere usually describing a bell-shaped curve whose central portion commonly is somewhat flattened; transverse ribs commonly offset at the midlines, reduced in height and deflected toward the aperture in the corner grooves, where they consist of a single row of longitudinally elongate nodes; transverse ribs number 5–11 per mm within about 10 mm of the apex, elsewhere 1–5 per mm. Rib nodes on the faces tend to be subhemispherical, closely spaced, numbering 5–13 per mm. Interspace ridges generally low, broad, distinctly wider than the interspace furrows on the faces proper; interspace ridges narrower and more closely spaced near and within the corner grooves; interspace ridges extend from the base of a rib node on the transverse rib nearest the aperture to an area between two adjacent rib nodes on the transverse rib nearest the apex; interspace furrows slightly raised along their axis; interspaces crossed by coarse, closely spaced longitudinal striae in the corner grooves; interspaces crossed by a band of fine longitudinal striae at the midlines. Apical end of some specimens covered by a schott.

Remarks. Conularia splendida was previously represented by a single specimen (GSC 2157, the holotype) from the English Head Formation (upper Ordovician) of Anticosti Island, Quebec. It is the only member of the genus *Conularia* known to exhibit a bifid carina or pair of carinae at the midlines.

Conularia? sp.

Plate 1, figure 3; Text-figure 3C

Material. SUI 84490 and 84491 (two specimens).

Horizon and Locality. Elgin Member, Lithosome II (Locality 18; specimens collected by Thomas N. Bayer, Winona State University, Winona, Minnesota).

Description. Two partial specimens, both moderately compressed and broken well above the apex, preserved as weathered casts exhibiting original test material in portions of the corners and midlines. Faces originally about equal in width. Corners of relatively undistorted faces diverge at about 18° on one specimen and about 25° on the other specimen; corners sulcate, external morphology of the corner grooves unknown. Transverse ribs gently arched or chevron-like on the faces, confluent or offset at the midlines; transverse ribs number 3–6 in a length of 2 mm. Interspace ridges moderately broad, in places aligned across the transverse ribs, elsewhere offset, with five ridges in a width of 1 mm on the faces proper; interspace ridges narrower and more closely spaced near and within the corner grooves; apertural end of the interspace ridges marked by a coarse, subhemispherical node. Corners and midlines carinate; carina continuous, broad, rounded; carina at the corners larger (broader and higher) than the carina at the midlines, with the corner carina extending up to roughly one-seventh of the distance to the centre of the test cavity.

Remarks. These specimens are provisionally identified as *Conularia* based on the presence of interspace ridges and nodose transverse ribs similar to those of *C. splendida* and *C. trentonensis*. However, these same features also characterize *Holoconularia* Hergarten, which differs from *Conularia* in having the transverse ribs disrupted and offset in the corner grooves (Hergarten 1985). Establishing the generic affinities of the two Elgin casts will therefore require the discovery of specimens preserving the corner grooves. The Elgin specimens differ from nearly all recognized members of *Conularia* (e.g. Slater 1907; Bouček 1928; Babcock and Feldmann 1986*b*; Babcock *et al.* 1987*b*) and *Holoconularia* (Hergarten 1985) in having a strong internal carina at the corners and midlines. A similar carina occurs at the corners and midlines of *C. albertensis* Reed (Devonian of South America and South Africa; Ulrich 1892, pl. 3, fig. 6a; Knod 1908, pl. 24, figs 1–2, pl. 31, fig. 3; Babcock *et al.* 1987*b*, fig. 10b), but in this taxon the transverse ribs are always continuous at the midlines (Babcock *et al.* 1987*b*).

Genus GLYPTOCONULARIA Sinclair, 1952

Glyptoconularia gracilis (Hall, 1847)

Plate 1, figure 5

1847 *Conularia gracile* Hall, p. 224, pl. 59, fig. 7.
1896 *Conularia gracilis* Hall; Ruedemann, pl. 11, figs 5–6.
1897 *Conularia gracilis* Hall; Ruedemann, pl. 2, figs 5–6.
1952 *Glyptoconularia gracilis* (Hall); Sinclair, p. 144.
1994 *Glyptoconularia gracilis* (Hall); Van Iten, p. 363, pl. 1.

Material. SUI 55065–55066 (two specimens); UMPC 8918, 07745 (two specimens).

Horizon and locality. Elgin Member, lower mixed faunas biofacies (Locality 2).

Description. Four specimens, all fragmentary. Corners sulcate, gently curved, diverging at *c.* 8°; corner grooves bear a low, broad, internal carina. Faces exhibit numerous, short, straight or adaperturally arching transverse ridges that are arranged in longitudinal files, with 4–6 files in a width of 1 mm and 7–9 transverse ridges in a length of 1 mm; lateral margins of the files marked by a low longitudinal ridge.

Remarks. Glyptoconularia is an extremely rare, monotypic genus currently known from middle and upper Ordovician strata of North America, where it has been found only in dark shales and lime mudstones (Van Iten 1994). Four of the eight reposited specimens of this genus are from brown and grey shales of the Elgin Member at Graf, Dubuque County, Iowa. In addition, we found possible *Glyptoconularia* fragments in acid residues from light grey lime mudstones in Lithosome II. Inspection of type specimens of *Glyptoconularia gracilis* in collections of the American Museum of Natural History, New York (AMNH 789) and the New York State Museum, Albany (NYSM 5063) revealed the presence of a very fine groove along the centre of the ridge bounding the longitudinal files (Van Iten 1994). Although such a groove is not evident in the Elgin specimens, we suspect that this is due to incomplete preservation and/or weathering of the original test material.

EXPLANATION OF PLATE 3

Figs 1–2. *Conularia trentonensis* Hall, 1847; SUI 61507; upper Ordovician, Maquoketa Formation, Elgin Member, ?Unit 3; north-eastern Iowa (Locality 16), USA. 1, part of the external surface of a single face showing the interspace bars (large arrow) and troughs (small arrow). 2, part of the external surface of a single corner groove and adjacent faces. Both ×25.

Figs 3–4. *Conularia splendida* Billings, 1866; upper Ordovician, Maquoketa Formation, Elgin Member, Unit 3; north-eastern Iowa (Locality 7), USA. 3, SUI 61521; a pair of low carinae straddling a midline; ×31. 4, SUI 61530; part of the external surface of a single face showing the interspace bars (large arrow) and troughs (small arrow); ×32.

All are scanning electron micrographs.


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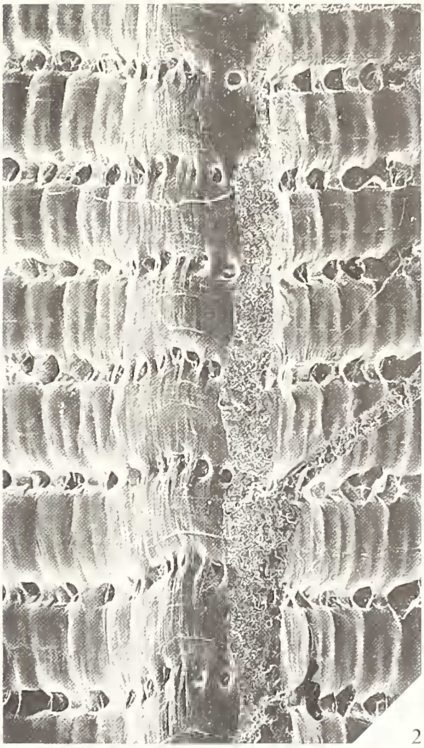
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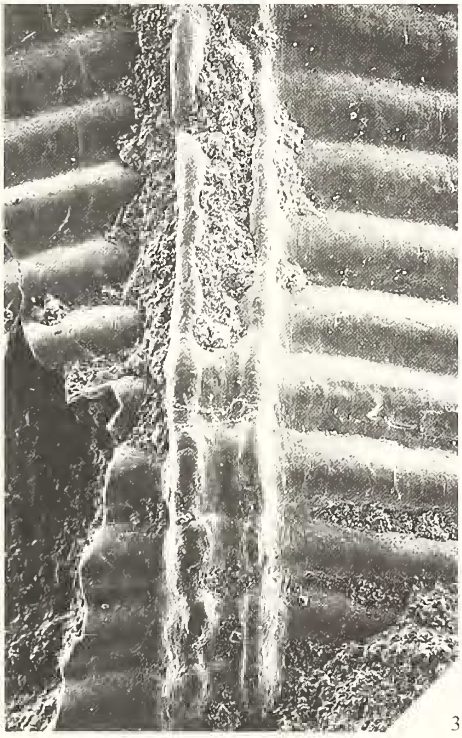
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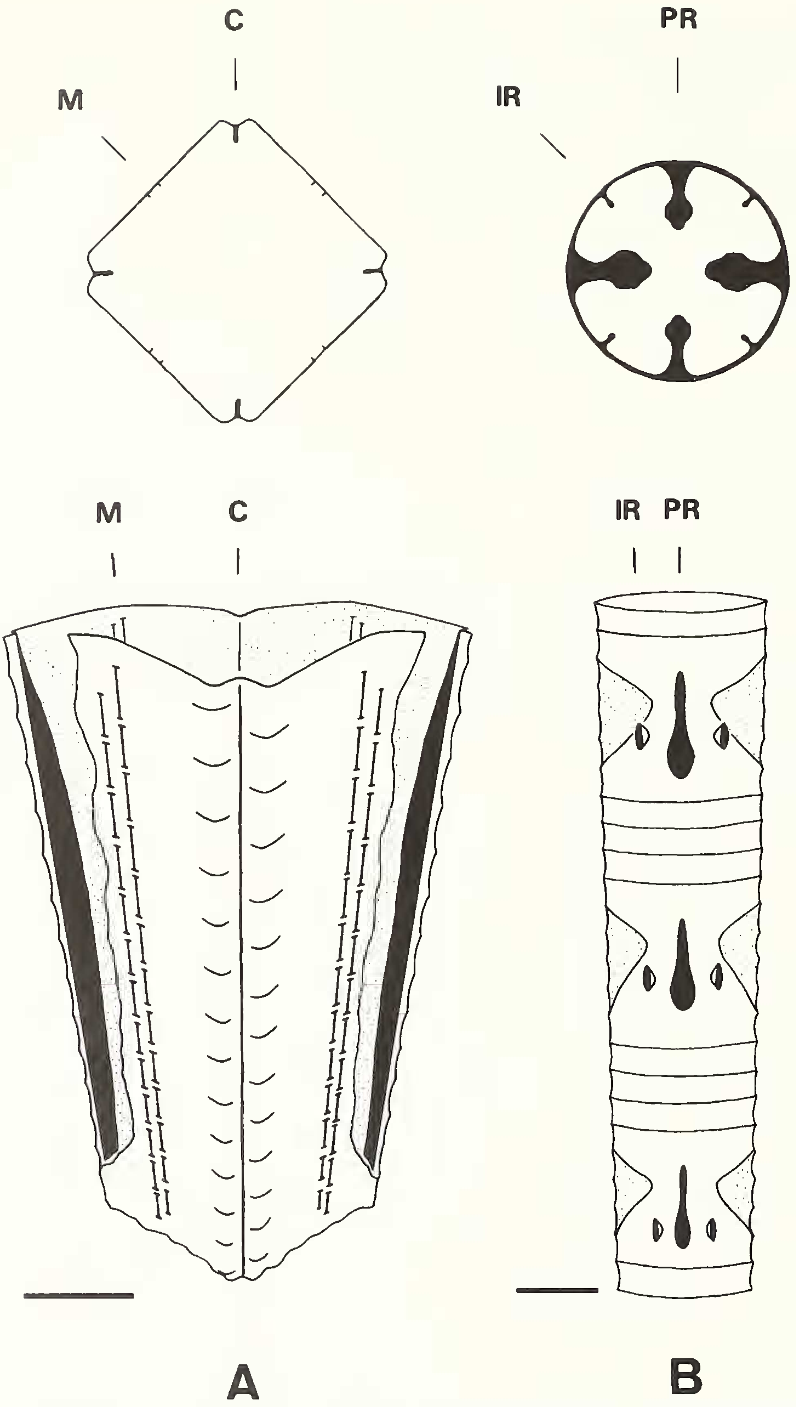
VAN ITEN *et al.*, *Conularia*



TEXT-FIG. 4. Comparison of the Elgin conulariid *Climacoconus sinclairi* sp. nov. and a theca of the coronatid scyphozoan polyp *Stephanoscyphus racemosus* Werner. A, partial reconstruction (bottom) and transverse section (top) of *Climacoconus sinclairi* showing the single high corner carina and the paired files of low, I-shaped ridges flanking the midlines; scale bar represents 1·5 mm. B, partial theca and transverse section of *Stephanoscyphus racemosus* Werner bearing several whorls of thorn-like internal projections; scale bar represents 1 mm; modified from Werner (1967, fig. 6b).

Genus METACONULARIA Foerste, 1928

Metaconularia heymani (Foerste, 1920)

Plate 2, figure 3

1920	*Conularia heymani* Foerste, p. 208, pl. 21, fig. 12; pl. 22, fig. 12.
1928	*Conularia heymani* Foerste; Foerste, p. 110.
1940	*Metaconularia heymani* (Foerste); Sinclair, p. 105, pl. 3, fig. 3.

Material. SUI 62672 and 84488 (two specimens); WSU unnumbered (one specimen).

Horizon and locality. Elgin Member, Lithosomes I and II (Localities 17b and 18), Units 1 and 3 (Locality 7).

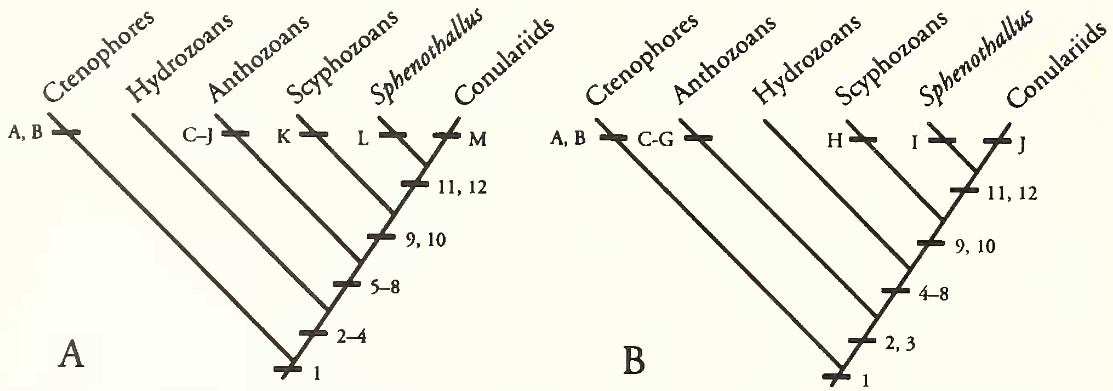
Description. Three specimens, one nearly complete, original length of the largest specimen exceeded 170 mm. Test thin, faces equal in width, corners of a given face diverge at *c.* 30°. Midlines non-sulcate; paired midline carinae low, narrow, diverging at slightly less than 0·5°. Nodes minute, hemispherical to subhemispherical and longitudinally elongate, arranged in transverse rows and longitudinal files, with the transverse rows tending to be more widely spaced than the longitudinal files; transverse rows bell-shaped on the faces, increasing in spacing and decreasing in degree of curvature away from the apex; transverse rows cross the corners and midlines without offset or diminution; transverse rows contain 10–38 nodes per mm, longitudinal files contain 6–23 nodes per mm.

Remarks. This is the first report of *Metaconularia heymani* from strata of late Ordovician age. This species, previously represented by two fragmentary specimens in collections of the United States National Museum, Washington, was first described from the middle Ordovician Plattin Formation near New London, Missouri, USA (Foerste 1920; Sinclair 1940).

CONULARIID CORNERS AND MIDLINES

In a previous article in this journal (Van Iten 1992*a*), the senior author discussed the anatomy and phylogenetic significance of internal test structures at the corners and midlines of conulariid tests. Among the conulariids reviewed in that article were *Climacoconus sinclairi* (identified as *Climacoconus* sp.; Van Iten 1992*a*, text-fig. 3G; scale bar in the earlier figure was incorrectly labelled as representing 5 mm; it represented 1 mm) and *Conularia splendida*, both from the Elgin Member. The discovery of an internal carina at the corners and/or midlines of three additional Elgin conulariids (*Climacoconus pumilus*, *C. quadratus* and *Conularia*? sp.) increases the already substantial number of conulariids known to exhibit such structures. Importantly, *Climacoconus quadratus*, *C. sinclairi* and *Conularia*? sp. exhibit an internal carina at both sites (Text-fig. 3). As in most other taxa having carinate corners and midlines, the carina at the corners of the three Elgin species is larger than the carina at the midlines.

Conulariid tests show detailed similarities to non-mineralized thecae of polypoid coronatid scyphozoans (e.g. Werner 1966, 1967; Van Iten 1991*a*, 1992*a*, 1992*b*). For example, the centripetally accreted, inner thecal lamellae of some coronatids are inflected in the perradial and interradial symmetry planes to form eight tetramerally arranged files of thorn-like internal projections (Text-fig. 4B). Projections in the perradial files, interpreted by Werner (1966, 1967) and Van Iten (1991*a*, 1992*a*, 1992*b*) as comparable to sulcate conulariid corners, are consistently larger than projections at the interradii, locally extending nearly all the way to the centre of the thecal cavity. Coronatid polyps possessing internal thecal structures are thus similar to conulariids whose corners and midlines are carinate. This is particularly evident in comparisons of projection-bearing coronatid thecae with the Elgin conulariid *Climacoconus sinclairi* (Text-fig. 4). Together with other uniquely shared similarities involving aspects of thecal structure and growth and damage repair (Werner 1966, 1967; Van Iten 1991*a*, 1992*b*; Jerre 1994), these gross anatomical similarities make the class Scyphozoa the best candidate for the nearest extant relative of conulariids (Text-fig. 5).



TEXT-FIG. 5. Cladograms summarizing two alternative hypotheses of phylogenetic relationships among conulariids, *Sphenothallus* and extant cnidarians. The cladograms summarize our interpretations of the affinities of the problematical taxa in the context of the two most widely accepted alternative interpretations of phylogenetic relationships among the extant cnidarian classes (Van Iten 1992*c*). In both cladograms ctenophorans (Phylum Ctenophora) are interpreted as the nearest living relatives of cnidarians. Many of the synapomorphies (numbered) involve soft-part structures that have not been observed in either conulariids or *Sphenothallus*, but that we infer to have been present in these two taxa based on observable similarities in other anatomical features. Those soft-part synapomorphies that we think can be observed in conulariids and/or *Sphenothallus* are indicated below by round brackets (presence of soft-part structure indicated by hard-part morphology) or square brackets (presence of soft-part structure indicated by relic (pyritized) soft parts; [ ] = conulariids, [ ]* = *Sphenothallus*). A, cladogram interpreting extant septate cnidarians as members of a monophyletic group that excludes non-septate cnidarians (hydrozoans) (cladogram modified from Van Iten 1992*a*, text-fig. 8). B, cladogram interpreting hydrozoans and scyphozoans as members of a monophyletic group that excludes anthozoans. Synapomorphies for cladogram A are as follows: 1, diploblastic, tentacle-bearing medusa with a non-septate digestive cavity having four radially disposed primary branches that bear the gonads; 2, cnidae (primitively with operculum and cnidocil); 3, planula larva; [4]*, life cycle with sessile polyp having two or more circumoral tentacles; 5, gastric septa; 6, cnidae-bearing gastric filaments; 7, sex cells ripen in the entoderm; 8, mesenchyme cellular; (9), four septa (e.g. Van Iten 1992*a*); [10], polydisc strobilation (Van Iten 1991*a*); 11, theca apatitic; 12, production of schotts that sometimes bear a subcentral dimple or protuberance. Autapomorphies (lettered) for cladogram A are as follows: A, cydippid larva; B, comb rows; C, loss of medusa; D, loss of cnidal operculum; E, loss of cnidocil; F, hexaradial and octaradial symmetry; G, actinopharynx; H, siphonoglyph; I, cnidae with tripartite flaps; J, cnidae with special ciliary cones; K, rhopalium; L, apatitic, tubular theca with two longitudinal thickenings; M, apatitic, four-sided steeply pyramidal theca. Synapomorphies (numbered) for cladogram B are as follows: 1, animal diploblastic and with radial symmetry in non-larval forms; 2, cnidae; 3, planula larva; 4, medusa; 5, cnidae with operculum; 6, cnidae with cnidocil; 7, mitochondrial DNA linear (Bridge *et al.* 1992); 8, polyp sheathed in a multilamellar, ectodermal theca having a closed basal attachment disc; (9), four septa; [10], polydisc strobilation (Van Iten 1991*a*); 11, theca apatitic; 12, production of schotts that sometimes bear a subcentral dimple or protuberance. Autapomorphies (lettered) for cladogram B are as follows: A, cydippid larva; B, comb rows; C, hexaradial and octaradial symmetry; D, actinopharynx; E, siphonoglyph; F, cnidae with tripartite flaps; G, cnidae with special ciliary cones; H, rhopalium; I, apatitic, tubular theca with two longitudinal thickenings; J, apatitic, four-sided steeply pyramidal theca.

Opponents of the hypothesis of a scyphozoan affinity for conulariids (e.g. Kozlowski 1968; Babcock and Feldmann 1986*a*; Babcock 1991; Yochelson 1991) have generally based their arguments on *differences* between conulariids and scyphozoans, including features purportedly present in conulariids and unique to them, rather than on rigorous demonstration of a set of shared derived *similarities* that support an alternative cladistic hypothesis. As a result of this exclusive focus on differences, advocates of this approach have tended to interpret conulariids as members of an independent extinct phylum. The logic of phylogenetic systematics, however, suggests that one of three criteria must be met before conulariids can be established either as a new phylum or as non-cnidarians: (1) there are no characters shared by conulariids with any other known phylum (i.e. there is no evidence to support a phylogenetic hypothesis at the phylum level); (2) the most parsimonious cladogram is an unresolved multichotomy, with the relationships of conulariids unresolved with respect to two or more phyla (i.e. the evidence does not allow for a choice among alternative phylum-level hypotheses); or (3) conulariids share a suite of derived similarities with a specific non-cnidarian taxon, and the cladogram depicting that set of relationships is more parsimonious than the cladogram placing conulariids and cnidarians as sister taxa (i.e. the evidence supports a *specific* alternative phylogenetic hypothesis).

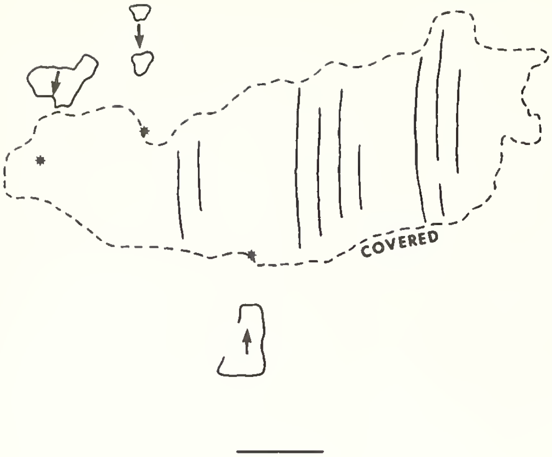
In order to evaluate alternative phylogenetic hypotheses, characters and character states must be rigorously identified, and alternative cladograms must be tested to determine which cladogram is the most highly corroborated by the evidence. Almost without exception, attempts to place conulariids in a separate phylum or remove them from Cnidaria have been based upon negative evidence (the alleged absence of phylogenetically informative characters) or upon an *arbitrary* judgement that the degree of difference between conulariids and other taxa is sufficient to warrant referring conulariids to their own phylum. A major problem has been the excessive focus on conulariid autapomorphies (e.g. Kozlowski 1968; Babcock and Feldmann 1986*a*), features that are of no use in analysing broader phylogenetic relationships. In the face of numerous similarities identified as being uniquely shared by conulariids and scyphozoan cnidarians (e.g. Kiderlen 1937; Werner 1966, 1967; Van Iten 1991*a*, 1992*a*, 1992*b*; Jerre 1994), in the absence of any demonstration that these similarities fail some critical test of homology (Patterson 1982: including tests of similarity, development, congruity, etc.), and in the absence of any more parsimonious alternative, conulariids must be classified as cnidarians (Text-fig. 5).

PALAEOECOLOGY OF ELGIN MEMBER *SPHENOTHALLUS* AND CONULARIIDS

Evidence of apical attachment in conulariids

A number of investigators (Finks 1955, 1960; Rooke and Carew 1983; Babcock *et al.* 1987*b*; Harland and Pickerill 1987; Lowenstam and Weiner 1989; Van Iten 1991*b*; Van Iten and Cox 1992) have presented evidence, some of it (Rooke and Carew 1983; Lowenstam and Weiner 1989) anecdotal, that conulariids were benthic organisms that spent at least part of their lives attached by their apex directly to the sea floor or to biological substrates such as mollusc shells and massive sponges. A similar mode of life has been proposed for *Sphenothallus* (Van Iten *et al.* 1992), based on discoveries of essentially complete *Sphenothallus* specimens attached to shell material together with discoveries of possible *Sphenothallus* holdfasts attached to hardground surfaces. A sessile benthic mode of life for conulariids is indicated most convincingly by two kinds of occurrences: clusters of erect conulariids preserved in Upper Carboniferous black shales (north-central Texas; Rooke and Carew 1983) and Silurian bioherms (north-eastern Illinois; Lowenstam and Wiener 1989); and clusters of conulariids preserved in massive sponges, with the conulariids oriented perpendicular to sponge growth surfaces and expanding (opening) away from the interior of the sponges (western Texas; Finks 1955, 1960; Van Iten 1991*b*).

Another line of evidence indicating conulariid apical attachment, although not necessarily to benthic substrates, is the occurrence of one or more conulariid specimens next to a piece of non-conulariid shell material in an orientation suggesting original attachment to it (e.g. Babcock *et al.* 1987*b*, fig. 4c; Van Iten 1991*c*, text-fig. 1A). This type of occurrence is exhibited by two groups of Elgin Member specimens. One of these groups consists of two specimens of *Climacoconus quadratus* associated with a partial *Sphenothallus* tubule (Pl. 1, fig. 5). The two conulariids, located next to and overlapping each other, are oriented at the same high angle to the tubule, and their apical ends lie on one of its edges. Although the conulariids do not preserve direct evidence of attachment to the tubule (their apices are missing), the probability of obtaining this and other, similar sets of spatial relationships between conulariids and non-conulariid shell material, under the null hypothesis that conulariids were *not* sessile, is essentially zero. The second association consists of four incomplete



TEXT-FIG. 6. *Conularia splendida* Billings; SUI 87728; upper Ordovician (Maquoketa Formation, Elgin Member, Unit 3); north-eastern Iowa (Locality 7), USA; camera lucida drawing of the outlines of three fragmentary specimens preserved next to a straight-shelled nautiloid. Arrows indicate the direction in which a specimen's apical end is pointing. Stars indicate the approximate position of a specimen's apex (now missing). Scale bar represents 20 mm.

specimens of *Conularia splendida* preserved next to a large, flattened, straight-shelled nautiloid (Text-fig. 6). Three conulariids, all located more or less in the same plane as the cephalopod, are oriented approximately perpendicular to the cephalopod's long axis and with their apical ends pointing toward the cephalopod. A fourth specimen, situated slightly below the plane containing the other three, also points toward the cephalopod but is inclined at a much lower angle to the cephalopod's long axis. Again, it is highly improbable that this association, with its multiple, spatial coincidences is fortuitous, particularly in light of previous descriptions of conulariid specimens and shell material showing similar relationships. Rather, it appears likely that these and other Elgin conulariids were attached in life to non-conulariid shell material and, possibly, other substrates.

Monospecific conulariid clusters

Climacoconus quadratus and *Conularia splendida*, two of the most abundant conulariids in the Elgin Member, commonly occur in monospecific clusters. Approximately one-quarter of the 125 specimens of *Conularia splendida* examined in this study occur in discrete, compact clusters of two to eight specimens, all situated within several millimetres of each other. Specimens in five of these clusters (e.g. Pl. 1, fig. 4) converge adapically on a common centre. Similar radial clusters (Van Iten and Cox 1992) have been documented from several other localities in the Palaeozoic of North America and Europe (e.g. Slater 1907, pl. 2, fig. 1; Ruedemann 1925, pl. 22, fig. 3; Sinclair 1940, pl. 2, fig. 5; Babcock and Feldmann 1986*a*, fig. 4), and have generally been interpreted as former life clusters formed either by clonal budding or by preferential larval settlement (Van Iten and Cox 1992). All of the Elgin Member radial clusters are from Units 1 and 3 of the trilobite-dominated biofacies. Coupled with evidence that conulariids were both sessile and benthic organisms, the occurrence of radial clusters in these two Elgin units suggests that *C. splendida* may have lived on the distal, dysoxic portion of the Elgin carbonate shelf. Had *C. splendida* been transported to this area from other parts of the shelf, then any life clusters probably would have been broken up during transport, and thus fossil remains showing radial arrangements would not occur in Units 1 and 3. Alternatively, Babcock and Feldmann (1984, 1986*b*) proposed that conulariids were planktonic or pseudoplanktonic organisms, an interpretation that implies that radial clusters preserved in dark mud rocks settled to the sea floor from the overlying water column. Evidence offered in support of this hypothesis consists of the observation that many conulariid species are widespread geographically or occur in strongly dissimilar lithofacies (Babcock and Feldmann 1986*b*), and also includes the discovery of a radial cluster of *Paraconularia chesterensis* (Worthen) associated with possible planktonic plant remains (Babcock and Feldmann 1986*b*, fig. 4). Although planktonic taxa generally do exhibit broad geographical ranges and/or occur in dissimilar facies, these observations alone do not constitute sufficient evidence of a planktonic or pseudoplanktonic lifestyle, for they do not rule out the hypothesis that conulariids were sessile benthic organisms capable of tolerating a wide range of bottom conditions.

Distribution of Sphenothallus *and conulariids*

Additional evidence bearing on the mode of life of conulariids and *Sphenothallus* is provided by statistical analysis of the distribution of collected Elgin fossils. As shown in Table 1, conulariids occur in all four Elgin biofacies, as does *Sphenothallus*. However, chi-square analysis of the data for

TABLE 1. Stratigraphical distribution and frequency of occurrence of collected Elgin Member *Sphenothallus* and conulariid macrofossils. Unit abbreviations: BMP, basal Maquoketa phosphorite; GSF, graptolite shales biofacies; MFF, mixed faunas biofacies; U1–U5, Units 1–5; LI–LIV, Lithosomes I–IV; LIIA, Lithosome II laterally equivalent to LI (Locality 19); LIIB, Lithosome II stratigraphically superior to LI (Localities 17 and 18). Underlined units are in the brachiopod-echinoderm biofacies, while units in brackets make up the trilobite-dominated biofacies. The letter symbol 'P' means the presence of a taxon in a unit is indicated by test fragments obtained from formic acid residues.

	Unit												
Taxon	BMP	GSF	MFF	[U1]	[U2]	[U3]	*U4*	*U5*	[LI]	*LIIA*	*LIIB*	*LIII*	LIV
Sphenothallus sp.	0	**4**	**6**	0	**P**	**P**	0	0	0	**50+**	**1**	0	0
Climacoconus pumilus	**45**	0	0	0	0	0	0	0	0	0	0	0	0
Climacoconus quadratus	0	0	0	**1**	0	0	**12**	**7**	**6**	**32**	**32**	**P**	0
Climacoconus sinclairi	0	0	0	0	**1**	**2**	0	**2**	0	0	0	0	0
Conularia splendida	0	**4**	**1**	**33**	**1**	**84**	0	0	**2**	0	0	0	0
Conularia trentonensis	0	**30**	**7**	0	0	0	0	0	**9**	**2**	**6**	**7**	0
Conularia? sp.	0	0	0	0	0	0	0	0	0	0	**2**	0	0
Glyptoconularia gracilis	0	**4**	0	0	0	0	0	0	0	0	**P**	0	0
Metaconularia heymani	0	0	0	**1**	0	**1**	0	0	**1**	0	**P**	0	0
Totals	45	42	14	35	2	87	12	9	18	84+	41	7	0

TABLE 2. 3 × 3 matrix for *Climacoconus quadratus*, *Conularia splendida* and *Conularia trentonensis* macrofossils collected from the brachiopod-echinoderm, trilobite-dominated and graptolite shales/mixed faunas biofacies. Application of the chi-square statistic to certain 2 × 2 contingency tables (e.g. *Climacoconus quadratus* and *Conularia splendida* in the brachiopod-echinoderm and trilobite-dominated biofacies) derived from the 3 × 3 matrix shows that the observed differences in the proportions of these three conulariids between the rock units are mostly highly significant, ruling out the null hypothesis that the distribution of these conulariids is independent of facies.

Example 2 × 2 comparison: for the proportions of *Climacoconus quadratus* and *Conularia splendida* macrofossils collected from the brachiopod-echinoderm and trilobite-dominated biofacies.

chi-square = $210(120(83))^2/(90)(120)(83)(127) = 182{\cdot}99 \gg 6{\cdot}635$, the chi-square value for the 0·01 level of probability.

	Brachiopod-echinoderm	Trilobite-dominated	Graptolite shales/mixed faunas	Totals
Climacoconus quadratus	83	7	0	90
Conularia splendida	0	120	5	125
Conularia trentonensis	15	9	37	61
Totals	98	136	42	276

conulariids reveals that the distribution of *Climacoconus quadratus*, *Conularia splendida* and *C. trentonensis* is facies-dependent (Table 2). Observed differences in the proportions of these three taxa between the mutually equivalent Elgin biofacies are statistically significant at the 0·01 probability level. For example, 83 of the 102 conulariid macrofossils collected from the brachiopod-echinoderm biofacies (Units 4 and 5 and Lithosomes II and III) represent *Climacoconus quadratus* (the remaining 19 specimens are either *Conularia*? sp. or *Conularia trentonensis*). In contrast, 120 of the 142 conulariid macrofossils collected from the trilobite-dominated biofacies (Units 1–3 and Lithosome I) are *Conularia splendida*. Only seven of these 142 specimens belong to *Climacoconus quadratus*. Similarly, 42 of the 46 conulariids collected in the Dubuque, Iowa area from the graptolite shales and lower mixed faunas biofacies also belong to *Conularia*, although 37 of these represent *C. trentonensis*. Not one of the 46 Dubuque area specimens represents *Climacoconus*. Differences in the proportions of *Climacoconus* and *Conularia* specimens are apparent in acid residue samples as well (Appendix 2). Whereas nearly all of the approximately 275 conulariid test fragments from Lithosome II represent *Climacoconus* or *Conularia trentonensis*, the 108 fragments from the trilobite-dominated biofacies consist predominantly of *Conularia*, probably *C. splendida* (as indicated by the relatively small size and close spacing of the rib nodes). Assuming that *Climacoconus* and *Conularia* had similar preservation potentials (as suggested by their similar test architectures and identical, chemically stable phosphatic composition), these results suggest that the proportions of the different conulariid taxa in the macrofossil samples accurately reflect the original relative abundances of these taxa in the Elgin sea. In addition, the fact that 19 of the 20 limestone blocks sampled here contained conulariid test fragments further suggests that conulariids are ubiquitous in the Elgin limestones.

Although the mode of life of fossil taxa probably can not be inferred from their distribution patterns alone (Klapper and Barrick 1978), the distribution patterns here observed are consistent with the hypothesis that conulariids were sessile benthic organisms, and they tend to falsify certain alternative interpretations of conulariid palaeoecology, in particular models interpreting conulariids as passive floaters or active swimmers living high in the water column. If conulariids were planktonic or nektonic and the distribution of conulariid taxa in life was independent of water depth and distance from the shoreline, the distribution of conulariid fossils would be independent of facies (all other factors being equal). If on the other hand the distribution of planktonic or nektonic conulariids was dependent on water depth and/or distance from the shoreline, the distribution of conulariid taxa could be facies-dependent (see for example Klapper and Barrick 1978, fig. 2a). The observation that *Climacoconus* is extremely rare in the sample from the trilobite-dominated biofacies and absent in the graptolite shales and mixed faunas samples, suggests that the observed distribution of Elgin conulariids cannot be attributed to simple depth segregation. If conulariid taxa were so segregated, with *Climacoconus quadratus* restricted to the oxic (upper) water mass and *Conularia splendida* occurring below this layer, one would expect to find substantial numbers of *Climacoconus* fossils in strata equivalent to the oxic-water brachiopod-echinoderm biofacies. Similarly, it is difficult to interpret Elgin conulariids as swimming or floating organisms subject to lateral segregation. Neither hypothesis, for example, offers a plausible explanation of how remains of originally planktonic or nektonic *Conularia trentonensis* could be present in oxic shelf and basin slope deposits but absent in deposits (Units 1–3) that formed in areas located between these two environments. In summary, then, the stratigraphical distribution of Elgin conulariids suggests that their distribution in life was controlled by bottom conditions, as might be expected had the conulariids lived on the sea floor or very close to it.

From this conclusion it follows that conulariids and, possibly, *Sphenothallus* were eurytopic taxa, capable of living in bottom environments where the concentration of dissolved oxygen may have been too low to support benthic invertebrates (e.g. echinoderms, bryozoans and articulate brachiopods) originally present in bottom waters located closer to the palaeoshoreline. In certain parts of the trilobite-dominated and graptolite shales biofacies, the only macrofossils present are nautiloids, asaphid trilobites and conulariids (*Isotelus iowensis*, *Anataphrus vigilans* and *Conularia splendida*; uppermost part of Unit 1, north-eastern Fayette County, Iowa; see also Calvin 1906,

p. 100) or inarticulate brachiopods, conulariids and *Sphenothallus* (certain grey shale horizons in the graptolite shales biofacies). Together with evidence suggesting that conulariids and *Sphenothallus* were sessile benthic organisms, the presence of these taxa in dark mudrocks lacking echinoderms and articulate brachiopods, taxa that are abundant in laterally equivalent shallow shelf strata, suggests that the problematical cnidarians inhabited dysoxic bottom environments. If the conulariid and *Sphenothallus* specimens now present in dysoxic facies were transported from the shallow shelf, then remains of other shelf taxa should also occur in these beds. Since the dysoxic facies generally do not contain such fossils, but do contain benthic invertebrates (*Lingula*) not present in more proximal deposits, the presence of conulariids and *Sphenothallus* in dark mudrocks of the trilobite-dominated, mixed faunas and graptolite shales biofacies probably cannot be attributed to transport from more proximal bottom environments. Therefore, unless Elgin Member *Sphenothallus* were attached in life to floating objects or to planktonic or nektonic organisms, the most likely explanation of the occurrence of conulariids and *Sphenothallus* in the distal Elgin Member facies is that these organisms originally inhabited dysoxic bottom waters of the shelf margin and basin slope environments.

Acknowledgements. The senior author thanks S. J. Boardman, C. E. Buchwald and K. O. Collier for their advice and encouragement during the initial stages of this study. T. J. Frest and B. J. Witzke commented on early versions of the manuscript and gave valuable advice on Elgin stratigraphy and depositional environments. Reviews by F. Jerre and one anonymous reader substantially improved the submitted version. Permission to borrow or examine museum specimens was granted by T. N. Bayer, D. Blake, T. E. Bolton, M. Carmen, F. J. Collier, M. Copeland, T. J. Frest, J. Golden, W. Hammer, W. F. Rice and R. Sloan. Many of the specimens now reposited in collections of the State University of Iowa (Iowa City) were collected by T. N. Bayer, A. C. Gerk, C. Levorson, O. Plocher and B. J. Witzke, who generously loaned them to us for study. We thank B. F. Glenister for taking the light photographs, and A. G. Becker, H. H. Tjarks and R. J. Van Iten for assistance in the field. Some of the scanning electron photomicrographs were taken by B. Wagner in the laboratory of H. T. Horner (Department of Botany, Iowa State University, Ames). This study was supported by funding from Sigma Xi and R. J. and H. B. Van Iten.

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Typescript received 8 August 1994
Revised typescript received 9 January 1996

APPENDIX 1

Selected collecting localities

1. Elgin Member, basal Maquoketa phosphorite and graptolite shales biofacies; active quarry (Riverside Stone Company) near Highway 20 in south-west Dubuque, Dubuque County, Iowa (NW1/4 NW1/4 sec. 33, T. 89 N., R. 2 E., Dubuque South, Iowa Quadrangle).
2. Elgin Member, graptolite shales and mixed faunas biofacies; road-cut on north-west side of gravel road, about 0·4 km south-west of Graf, Dubuque County, Iowa (near centre S1/2 NW1/4 SW1/4 sec. 29, T. 89 N., R. 1 E., Epworth, Iowa Quadrangle).
3. Elgin Member, graptolite shales biofacies; abandoned quarry in Osborne Park/Nature Center (Clayton County, Iowa), about 200 m east-north-east of State Highway 13 bridge over Volga River (quarry exposes upper part of Dubuque Formation and lower Elgin Member, with contact between these units occurring roughly 6 m above quarry floor; near centre NE1/4 SW 1/4 sec. 9, T. 92 N., R. 5 W., Elkader, Iowa Quadrangle).
4. Elgin Member, basal Maquoketa phosphorite, Units 1–3; abandoned quarry on east side of north–south gravel road, about 2 km north of Big Springs Trout Hatchery, Clayton County, Iowa (quarry exposes contact between Maquoketa and Dubuque formations; near western edge NW1/4 NW1/4 sec. 26, T. 94 N., R. 6 W., Gunder, Iowa Quadrangle).
5. Elgin Member, Units 2–4; roadcut and abandoned quarry on south-east side of County Road B64, about 5·6 km east-south-east of Elgin in extreme north-west Clayton County, Iowa (W1/2 SE1/4 SW 1/4 sec. 16 (road-cut) and E1/2 NE1/4 NW1/4 sec. 21 (road-cut and quarry), T. 94 N., R. 6 W., Gunder, Iowa Quadrangle).
6. Elgin Member, Units 3–5; road-cut and small abandoned quarry on east side of gravel road, about 4 km east-south-east of Elgin in extreme north-west Clayton County, Iowa (SE1/4 SW1/4 SW1/4 sec. 17, T. 94 N., R. 6. W., Gunder, Iowa Quadrangle).
7. Elgin Member, Units 1–4; road-cut on north-east side of County Road B64, about 1·6 km east-south-east of Elgin along the Fayette/Clayton County line, Iowa (E1/4 SE1/4 sec. 13, T. 94 N., R. 7 W., Elgin, Iowa Quadrangle).
8. Elgin Member, Units 3 and 4; small abandoned quarry in hillside overlooking east bank of Turkey River, about 2 km north-north-east of Elgin, Fayette County, Iowa (Gilbertson Wildlife Area; NE1/4 SW1/4 SW1/4 sec. 12, T. 94 N., R. 7 W., Gunder, Iowa Quadrangle).
9. Elgin Member, Unit 1; stream-cut near mouth of Bell Creek, about 1·6 km south of Clermont, Fayette County, Iowa (SW 1/4 SW 1/4 SW1/4 sec. 3, T. 94 N., R. 7 W., Elgin, Iowa Quadrangle).
10. Elgin Member, Units 4 and 5; road-cut on north-east side of gravel road along Bell Creek, next to bridge over Bell Creek and about 1·6 km south-south-west of Clermont, Fayette County, Iowa (N1/2 SE1/4 SE1/4 sec. 4, T. 94 N., R. 7 W., Elgin, Iowa Quadrangle).
11. Elgin Member, Units 3–5; road-cut on south-east side of Highway 18 near base of Montauk Hill, Clermont, Fayette County, Iowa (near centre E1/4 NE1/4 NE1/4 sec. 34, T. 95 N., R. 7 W., Castalia, Iowa Quadrangle).
12. Elgin Member, Unit 3; stream-cut on north-east side of eastward-flowing tributary of Fitzgerald Creek, about 6·4 km north-north-west of Clermont, Fayette County, Iowa (near centre SE 1/4 sec. 8, T. 95 N., R. 7 W., Castalia, Iowa Quadrangle).
13. Elgin Member, Units 3 and 4; road-cut on south-east side of County Road W42, about 13 km north-north-east of West Union, Fayette County, Iowa (SW1/4 NW1/4 SW 1/4 sec. 3, T. 95 N., R. 8 W., Festina, Iowa Quadrangle).
14. Elgin Member, Unit 3; road-cut on north-west side of gravel road, about 0·4 km west of bridge over Dibble Creek and about 9 km north-north-east of Clermont, Fayette County, Iowa (near centre NE1/4 sec. 2, T. 95 N., R. 7 W., Castalia, Iowa Quadrangle).
15. Elgin Member, basal Maquoketa phosphorite; active quarry (exposing Dubuque Formation as well as lower Maquoketa Formation) on east side of Highway 51, about 5 km north of Postville, Allamakee County, Iowa (SW 1/4 SW 1/4 SW 1/4 sec. 16, T. 96 N., R. 6 W., Frankville, Iowa Quadrangle).
16. Elgin Member, Lithosomes I and II; active quarry (Bigalk Quarry) 9·6 km north of north-east corner of Cresco, Howard County, Iowa (near north-west corner sec. 24, T. 100 N., R. 7 W., Cresco NE, Iowa Quadrangle).

17a–b. a, Elgin Member, Lithosome I; road-cut on north side of gravel road, approximately 0·5 km west-north-west of Granger, Fillmore County, Minnesota (SW1/4 NW 1/4 sec. 34, T. 101 N., R. 11 W., Greenleafton, Minnesota-Iowa Quadrangle). b, Elgin Member, Lithosome II; road-cut on north side of gravel road, approximately 1 km west-north-west of Granger, Fillmore County, Minnesota (NE1/4 NE1/4 sec. 33, T. 101 N., R. 11 W., Greenleafton, Minnesota-Iowa Quadrangle).

18. Elgin Member, Lithosomes I and II; bluff and ravine along east bank of Upper Iowa River, approximately 3 km west of Granger, Fillmore County, Minnesota (SW1/4 SW1/4 SE1/4 sec. 32, T. 101 N., R. 11 W., Greenleafton, Minnesota-Iowa Quadrangle).

19. Elgin Member, Lithosome II; active quarry (Rifle Hill Quarry) and road-cuts approximately 11 km east of junction of US Highway 63 and Fillmore (Minnesota) County Road 14, Fillmore County, Minnesota (NE1/4 NW1/4 sec. 35, T. 102 N., R. 12 W., Greenleafton, Minnesota-Iowa Quadrangle).

APPENDIX 2

Numbers of *Sphenothallus* and conulariid test fragments recovered from one kilogramme Elgin limestone slabs digested in formic acid. Letter symbols are as follows: N_{sp}, number of *Sphenothallus* fragments; N_{Cl}, number of *Climacoconus* fragments; N_{Co}, number of *Conularia* fragments; N_{Gl}, number of *Glyptoconularia* fragments; N_{Me}, number of *Metaconularia* fragments. Number in brackets behind the first, or stratigraphically lowest sample (numbered 0) from a given locality is the height in metres of that sample above the base of the unit or lithosome from which it was collected. All other sample numbers correspond to the approximate height of a given sample above the lowest sample. Additional phosphatic test material recovered from Elgin Member limestone samples consisted of conodonts and is not included in this table.

Locality/sample	*Unit*	N_{sp}	N_{Cl}	N_{Co}	N_{Gl}	N_{Me}	Total
4/0 [1 m]	Unit 1	0	0	0	0	0	0
4/1	Unit 1	1	0	0	0	0	1
4/3	Unit 2	1	2	15	0	1	18
4/4	Unit 2	0	3	12	0	0	15
4/5	Unit 3	1	0	5	0	0	6
4/6	Unit 3	0	0	1	0	0	1
4/7	Unit 3	0	2	1	0	0	3
4/9	Unit 3	2	1	56	0	2	61
8/?	Unit 2	2	3	5	0	0	10
16/?	Lithosome III	2	2	112	0	0	114
17/0 [1 m]	Lithosome IIB	0	3	3	0	0	6
17/1	Lithosome II B	10	0	1	0	0	11
17/2	Lithosome IIB	5	30	3	6	0	44
17/3	Lithosome IIB	1	4	0	2	3	10
17/4	Lithosome IIB	3	16	2	9	0	30
17/5	Lithosome IIB	0	3	0	2	0	5
17/6	Lithosome IIB	0	1	0	0	0	1
19/1 [1 m]	Lithosome IIA	0	1	14	0	0	15
19/2	Lithosome II A	2	1	1	0	0	4
19/3	Lithosome IIA	10	52	2	3	0	67